Bollettino Malacologico, Vol. 32 N° 1-4, pp 79-88, 1996
Stampato in Italia, Milano15 settembre 1997

Società Italiana di Malacologia
Lavoro accettato il 24 ottobre 1995

BIOGEOGRAPHICAL PATTERNS IN DEVELOPMENTAL STRATEGIES OF GASTROPODS FROM MEDITERRANEAN *POSIDONIA* BEDS*

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MARCO OLIVERIO. 1996. Biogeographical patterns in developmental strategies of gastropods from mediterranean *Posidonia* beds- *Boll. Malac.* **32** (1-4): 79-88.

KEY WORDS: *Posidonia oceanica*, development, gastropods, Ecology, Mediterranean, Evolution, palaeoclimate.

Abstract: The faunistic composition of *Posidonia oceanica* (L.) Delile beds from four areas of the Mediterranean basin has been studied, with special reference to the prosobranch component. Southern Spain was selected as typical of the Western Mediterranean, Ischia Is. (Italy) as typical of Central Mediterranean; Datcha (Turkey) as typical of the Aegean Sea and Yenikas (Turkey) as typical of the Levant basin. The results of this preliminary survey seem to verify the hypothesis that a gradient along an W-E axis does exist with respect to the developmental strategies of the caenogastropods. Excluding the archaeogastropos (systematically biased toward a NP development), the percentage on planktotrophic species decreases whilst that of the non-planktotrophic species increases along a W-E longitudinal transect. Palaeoclimatic events could have been responsible of the partitioning of species and populations of caenogastropods according to their larval development. Especially cooling phases in the Quaternary are very likely to have had remarkable effects in this sense.

Riassunto: I Molluschi (ed in particolare i Conchifera) sono degli ottimi indicatori delle caratteristiche biologiche delle comunità cui appartengono. La quantità di informazioni contenute nella sola conchiglia permette di studiare individui morti o resti fossili, e offre la possibilità (unica nel Regno Animale) di investigare lo sviluppo larvale di un individuo studiandone l'adulto (se la conchiglia embrionale/larvale è preservata). Si presentano quindi (in particolare i gasteropodi) come buoni soggetti per investigare patterns evolutivi nello spazio e nel tempo. Nel presente lavoro si sono studiate le composizioni faunistiche di praterie di *Posidonia oceanica* (L.) Delile da quattro località del Mediterraneo, con particolare riguardo alla componente a prosobranchi: Spagna meridionale come rappresentante del Mediterraneo occidentale, Ischia del Mediterraneo centrale, Datcha e Yenikash rispettivamente del Mar Egeo e del bacino Levantino. I risultati di questo studio preliminare, sembrano verificare l'esistenza di un gradiente Ovest-Est per lo sviluppo larvale dei prosobranchi cenogasteropodi della comunità della *Posidonia oceanica*. Escludendo infatti gli archeogasteropodi (primitivamente solo a sviluppo non-planctotrofico), si osserva un netto aumento della percentuale di specie non-planctotrofiche lungo un transetto longitudinale Ovest-Est. Probabilmente eventi paleoclimatici che si ritengono responsabili di aver influito sulla microevoluzione (speciazione associata alla perdita della planctotrofia) di singole specie, possono aver operato con effetti similari (ripartizione di specie e popolazioni) sulle comunità. In particolare fasi fredde nel Quaternario hanno molto probabilmente avuto effetti rimarchevoli in tal senso.

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Introduction

Molluscs are a very diverse group, adapted to many (nearly all) environments in the marine realm, and are very good marker of biological features of the communities to which they belong. The conchiferans, and particularly the gastropods, are especially suitable to this aim.

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* This work was presented at the First Workshop on Marine Molluscan Communities of the Mediterranean Sea, held in Gibilmanna (Palermo, 7-9 October, 1994)

The amount of information contained even in the sole shells allows e.g. study dead specimens and even fossil rests, or desume developmental patterns of the individuals by examining the adults, if the embryonic/larval shells are preserved. Caenogastropods offer a powerful tool to investigate evolutionary patterns over time and space. These so-called 'higher prosobranchs' developed a planktotrophic larval stage as an important evolutionary novelty that greatly contributed to their success (HASZPRUNAR, 1988). Notwithstanding, this phase has been repeatedly lost in many lineages. The presence of either larvae with a long pelagic life, or a short or absent pelagic larval phase, exert a remarkable influence on the life history of a species, especially as concerns their dispersal capability, the possibility and the extent of gene flow between populations, as well as the extinction rate (MILEIKOVSKY, 1971; SCHELTEMA, 1972, 1977; SHUTO, 1974; VALENTINE & JABLONSKI, 1986). Generally, developmental types can fall into two fundamental categories (JABLONSKI & LUTZ, 1980, 1983): 1 planktotrophic [P], with larvae feeding on plankton and spending a relatively long time in the planktonic stage. 2 non-planktotrophic [NP]: mostly lecithotrophic, but including also direct development, brooding etc.; larvae, if present (lecithotrophic), have at their disposal a more or less large yolk supply, reach metamorphosis without feeding on plankton and usually spend a lesser, or no time at all, in the plankton.

It is known (OLIVERIO, 1991, 1994a, 1995a) that many pairs of sibling/cryptic species, differing only or mainly in the respective larval development (planktotrophic vs. non-planktotrophic), have the non-planktotrophic representative mainly distributed in the Eastern basin. The present survey is the first step of a study directed to verify the hypothesis that also communities were affected by the same factors, and to define what effects were produced on the assemblages, with respect to larval developmental types. The study is still in progress, and a further report will include a larger dataset, in terms of sites and seasonal sampling.

Gastropods are typical of and abundant in two general environments: the algal biocoenoses and the seagrass beds. The algal biocoenoses are a very diverse complex of faunistic assemblages whose structures and patterns are difficult to approach over time and space dimensions. Therefore, algal communities have been considered to be unsuitable to be studied in the present survey due to their high degree of heterogeneity, even over spatial microscale, and the limited amount of time and equipment available for sampling in the eastern basin.

The *Posidonia oceanica* (L.) Delile benthic community is a well-structured assemblage of species, more homogeneous through the whole Mediterranean, even from the faunistic point of view. It is possible to consider it as an unit over the whole basin, surveyable over time and space, and approachable in this preliminary survey even with limited means.

Material and methods

The faunistic composition of *Posidonia oceanica* beds from four areas of the Mediterranean basin has been studied, with special reference to the prosobranch component (Fig. 1). All data refer to the leaf stratum of the seagrass beds. Southern Spain was selected as typical of the western Mediterranean, Ischia Is. (Italy) as typical of central Mediterranean; Datcha (Turkey) as typical of the Aegean Sea and Yenikash (Turkey) as typical of the Levant basin. The list for Ischia are based on personal sampling and on Russo *et al.* (1986); data for southern Spain are based on TEMPLADO (1984). The lists for the eastern Mediterranean sites arise from non quantitative sampling carried out during the AKDENIZ'92 expedition (OLIVERIO *et al.*, 1993). Nomenclature is mostly based on SABELLI *et al.* (1990-1992). Data set is in the form of simple contingency (presence/absence) tables of species. Similarity among the sites are calculated by the Jaccard index, and the pattern shown by an UPGMA dendrogram.

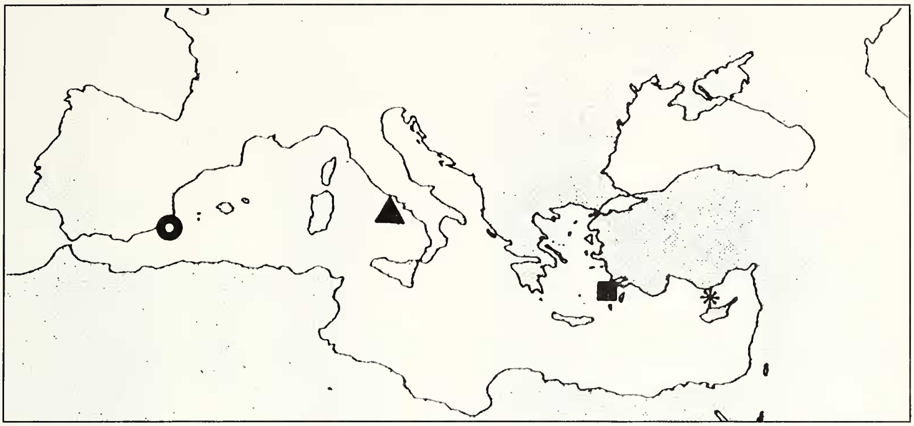

Figure 1. Location map of the study sites: circle = Cabo de Palos (Murcia, Spain: after Templado, 1984); triangle = Ischia (Italy: after Russo *et al.*, 1986 and personal sampling); square = Datcha (Turkey; AKDENIZ'92 expedition, Oliverio *et al.* 1993); asterisk = Yenikash (Turkey; AKDENIZ'92 expedition, Oliverio et al. 1993).

Subsequently the larval development of the species in the communities has been analysed to discover the possible presence of gradients along an E-W axis. All archaeogastropods (excluding the neritid *Smaragdia viridis*) have a non-planktotrophic development. The larval development of each caenogastropod species was defined according to the shape and dimensions of its protoconch. Presence/absence of an embryonic shell and comparative use of dimension vs. number of whorls allowed to define the type of larval development of caenogastropods (Figs. 2-5; Jablonski & Lutz, 1980; Oliverio, 1994a). The percentage of NP species was calculated either including or excluding the exclusively NP archaeogastropods. This procedure should allow to evaluate if a systematic bias altered detection of geographic pattern.

Results

Table I reports the lists of the species with their presence/absence in each site, and their larval development (planktotrophic vs. non-planktotrophic). Names used in literature to identify planktotrophic vs. non-planktotrophic 'forms' in pairs of suspected sister species have been employed when available (*e.g.*, *Rissoa monodonta* and *R. auriformis*, or *R. auriscalpium* and *R. rhodensis, R. italiensis* etc.). Otherwise the term -complex has been used (e.g. *R. violacea*-complex). An UPGMA tree (Fig. 6) displays the degree of similarity among the sites, based on the Jaccard index of similarity calculated after the contingency table. In the easternmost site (Yenikash), it is noteworthy the abundance of at least two Indo-Pacific species, recently introduced in the Mediterranean Sea by two different way (i.e. *Strombus persicus* [a man introduced species] and *Anachis savignyi* [a lessepsian migrant], both with planktotrophic development) in the *Posidonia* beds of the Levant basin (see Oliverio, 1995).

Two pairs of figures for each sites are reported (Tables II and III) to show the percentage of P vs NP: the first refers to the whole list (including the archaeogastropods), the second refers to the sole caenogastropods. In Figures 7 and 8 histograms are depicted according to the percentage of NP vs. P species in each site (archaeogastropods included and excluded respectively).

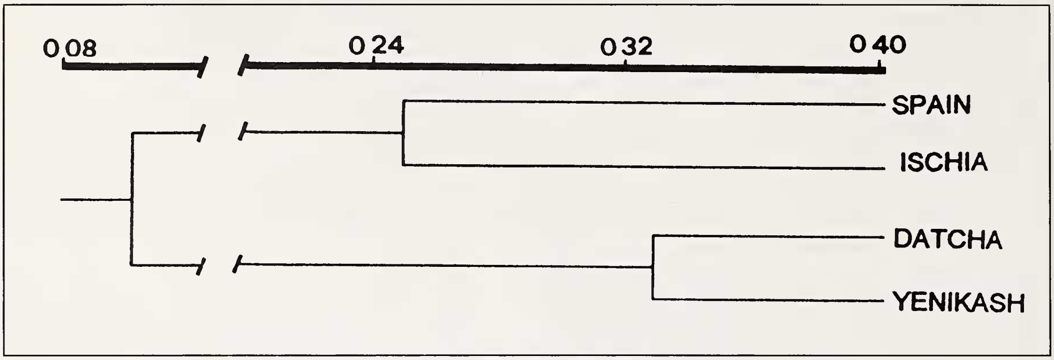

Figure 6. UPGMA tree portraying similarity pattern (Jaccard index) between the study sites.

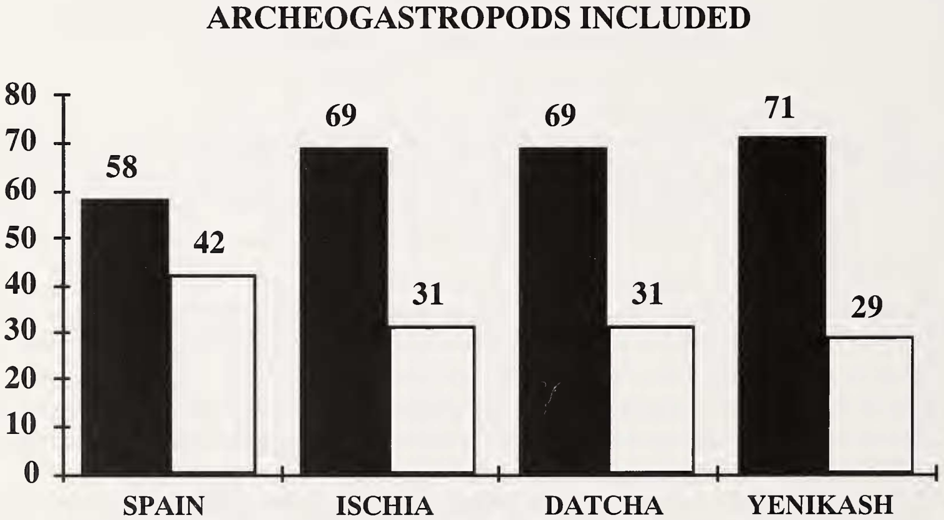

Figure 7. Diagrams showing the percentage of non-planktotrophic (black bars) vs. planktotrophic (white bars) species in the study sites (figures are the % of the relative bar). Archaeogastropods included.

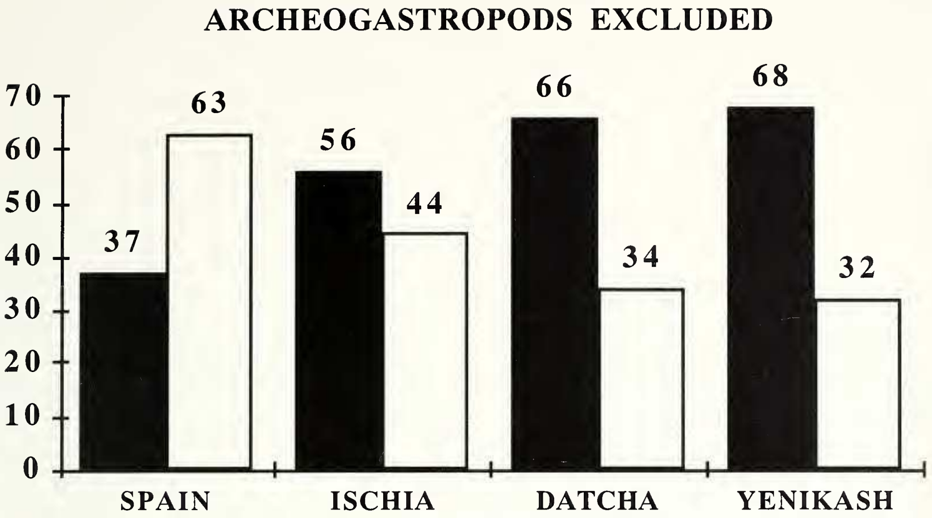

Figure 8. Diagrams showing the percentage of non-planktotrophic (black bars) vs. planktotrophic (white bars) species in the study sites (figures are the % of the relative bar). Archaeogastropods excluded.

Discussion

The UPGMA pattern is perfectly in agreement with the geographical location of the study sites. The analysis of the larval development on the whole faunistic list does not reveal any noticeable pattern (Table II and Fig. 7). It is noteworthy that the archaeogastropods are more abundant in the western sites. Excluding the exclusively lecithotrophic archaeogastropods the pattern is different (Table III and Fig. 8). The western and central Mediterranean lists contain higher percentage of species with planktotrophic development. The two Eastern Mediterranean sites studied, displayed an increasing dominance of non-planktotrophic developing species. The results of this preliminary survey seem to show a gradient along a W-E longitudinal transect, with respect to the developmental strategies of the gastropods. Percentage of non-planktotrophic species increases along a W-E axis.

Recent genetic studies on two rissoid complexes related to the *Posidonia oceanica* community (the *Rissoa auriscalpium* and the *R. violacea* complex, respectively) indicated a very low level of divergence between the Aegean populations (with non-planktotrophic development) and the Tyrrhenian ones (with planktotrophic development) of both complexes (OLIVERIO, 1994b). It has been suggested there that very Recent palaeoclimatic events could have been responsible of the partitioning of species and populations according to their larval development. Especially, cooling phases in the Pleistocene, and sea-level changes during the Holocene are very likely to have had remarkable effects in this sense (OLIVERIO, 1996b).

The study of the evolutionary aspects of larval ecology from the community point of view strengthen the hypothesis that biological parameters are more directly correlated to the evolution of larval development. Variation in one of such parameters (i.e. species ranges, predation rate, food availability, etc.) can be considered as a main factor (see STRATHMANN, 1978a, b, 1985; Oliverio1996a). Physical factors (temperature, salinity, oxygen concentration, etc.) can be responsible of altering one or several of the above biological parameters, and in some way also the habitat complexity. Similar trends toward the loss of a planktotrophic larval phase can be detected in areas affected by opposite measures of physical factors (e.g.: Gulf of Gabès [high temperature/salinity] vs. Baltic Sea [low temperature/salinity]: both sites can be characterised by e.g. high predation rate, low food availability, resticted ranges by water incirculation and low depth etc.). The above notes are the working hypothesis upon which future studies will be based. It is here further suggested that short term vs. long term fluctuations of physical parameters probably work in different ways, though inteconnected, affecting the evolution of both species and communities. For instance, structural changes not geographically correlated (e.g. those depending on depth gradients: see Russo, 1989) will be of relevant interest, while studying the functional adaptations of the communities, along the smaller temporal scale of the ecological changes. The definition of such differences and of the interconnections, can allow to better understand the mechanisms of evolution of the benthic assemblages in the mediterranean seas.

Acknowledgements

Renato Chemello is acknowledged for his invitation to the workshop. The participants to the AKDENIZ'92 Expedition are here heartily acknowledged: particularly, Raimondo Villa collaborated during collecting at Datcha and Yenikash. Paola La Valle was very skillful in sorting out the Turkish material and helped with bibliographic research. The AKDENIZ'92 Expedition was funded by MURST (40% funds). Work partly supported by CNR (Comitato Ambiente) funds.

Table I. List of the species with their presence(+)-absence(-) in each study site. For each species the inferred larval development is reported: P = planktotrophic, NP = non-planktotrophic. The blank line separates the archaeogastropods from the caenogastropods.

ARCHAEOGASTROPODA	Dev..	SPAIN	ISCHIA	DATCHA	YENIKASH
Scissurella costata (D'Orbigny, 1824)	NP	-	+	-	-
Emarginula sp.	NP	-	+	-	-
Smaragdia viridis (L., 1758)	P	-	-	+	+
Clanculus cruciatus (L., 1758)	NP	+	-	-	-
Clanculus jussieui (Payr., 1826)	NP	+	+	-	-
Calliostoma conulum (L., 1758)	NP	-	+	-	+
Calliostoma laugieri (Payr., 1826)	NP	+	+	-	-
Calliostoma zyzyphinum (L., 1758)	NP	-	-	-	+
Gibbula adansoni (Payr., 1826)	NP	-	+	-	-
Gibbula ardens (Von Salis, 1793)	NP	-	+	+	+
Gibbula richardi (Payr., 1826)	NP	-	+	-	-
Gibbula tumida (Montagu, 1803)	NP	+	-	-	-
Gibbula umbilicaris (L., 1758)	NP	+	+	-	-
Jujubinus aegensis Nordsieck, 1973	NP	-	-	+	-
Jujubinus exasperatus (Pennant, 1777)	NP	+	+	+	+
Jujubinus striatus (L., 1758)	NP	-	+	-	-
Homalopoma sanguineum (L., 1758)	NP	-	+	-	-
Tricolia pullus (L., 1758)	NP	+	+	-	+
Tricolia speciosa (Von Muehlfeldt, 1824)	NP	+	+	+	-
Tricolia tenuis (Michaud, 1829)	NP	-	+	-	-

CAENOGASTROPODA	Dev..	SPAIN	ISCHIA	DATCHA	YENIKASH
Bittium jadertinum (Brusina, 1865)	P	-	-	+	-
Bittium latreillei (Payr., 1826)	P	+	+	+	+
Cerithium vulgatum Bruguière, 1832	P	-	-	+	+
Vermetus cfr.*granulatus* (Gravenhorst, 1831)	P	-	+	-	-
Turritella turbona Monts., 1877	NP	-	-	+	+
Eatonina cossurae (Calcara, 1841)	NP	-	+	-	-
Eatonina fulgida (Adams J., 1797)	NP	-	+	-	-
Alvania aspera (Philippi, 1844)	NP	-	-	+	-
Alvania cimex (L., 1758)	P	+	-	-	-
Alvania colossophilus Oberling, 1970	NP	-	-	+	+
Alvania discors(Allan, 1818)	NP	-	+	-	-
Alvania lineata Risso, 1826	NP	+	+	-	-
Alvania mamillata Risso, 1826	NP	-	-	+	-
Pusillina lineolata (Michaud, 1832)	P	-	+	-	-
Pusillina munda (Monts., 1884)	NP	-	-	+	+
Pusillina philippii (Aradas & Magg., 1844)	P	+	+	-	-
Pusillina radiata (Philippi, 1836)	P	-	+	-	-
Pusillina sp.A	P	-	-	+	+
Pusillina sp.B	P	-	-	+	+
Rissoa auriformis Pallary, 1804	NP	-	-	+	-
Rissoa auriscalpium (L., 1758)	P	+	+	-	-
Rissoa decorata Philippi, 1846	P	+	-	-	-
Rissoa guerini Récluz, 1843	P	+	+	-	-
Rissoa italiensis Verduin, 1985	NP	-	+	-	-
Rissoa monodonta Philippi, 1836	P	+	-	-	-
Rissoa rhodensis Verduin, 19885	NP	-	-	+	+
Rissoa variabilis (Von Muehlfeldt, 1824)	NP	+	+	-	+
Rissoa ventricosa (Desmarest, 1814)	P	+	+	+	-
Rissoa violacea (Desmarest, 1814)	P	+	+	-	-
Rissoa violacea-complex	NP	-	-	+	-
Rissoina bruguierei (Payr., 1826)	P	+	-	+	-
Barleeia unifasciata (Montagu, 1803)	NP	-	+	-	-
Nodulus contortus (Jeffreys, 1856)	NP	-	+	-	-
Caecum auriculatum De Folin, 1868	P	-	+	-	-
Strombus persicus Swainson, 1821	P	-	-	-	+
Monophorus perversus (L., 1758)	P	-	+	-	-
Cerithiopsis barleei Jeffreys., 1867	P	-	-	+	-
Cerithiopsis minima (Brusina, 1865)	P	-	-	-	+
Cerithiopsis sp.	P	-	-	-	+
Cerithiopsis tubercularis (Montagu, 1803)	P	-	+	-	-
Melanella polita (L., 1758)	P	-	+	-	-
Parvioris microstoma (Brusina, 1864)	P	-	+	-	-
Vitreolina philippi (De Rayn.,V.d.-Hec. Pon.,	P	-	+	-	-
Ocinebrina aciculata (Lamarck, 1822)	NP	+	+	+	-
Dermomurex scalaroides (Blainville, 1829)	NP	-	-	-	+
Hexaplex trunculus (L., 1758)	NP	-	+	+	+
Muricopsis cristata (Brocchi, 1810)	NP	+	+	-	+
Chauvetia sp.	NP	-	-	+	-
Chauvetia submamillata (BDD, 1882)	NP	-	-	+	-
Chauvetia brunnea (Donovan, 1804)	NP	+	+	-	-
Engina leucozona (Philippi, 1843)	NP	-	-	+	-
Buccinulum corneum (L., 1758)	NP	-	+	+	+
Fusinus pulchellus (Philippi, 1844)	NP	-	+	-	-
Fusinus syracusarus (L., 1758)	NP	-	+	+	-
Fusinus sp.	NP	-	-	-	+

Nassarius incrassatus (Stroem, 1768)	NP	-	-	-	+
Mitrella gervillei (Payr., 1826)	NP	-	+	-	-
Anachis sanignyi Moazzo, 1939	P	-	-	-	+
Columbella rustica (L., 1758)	NP	-	+	-	+
Mitrella scripta (L., 1758)	NP	-	-	-	+
Vexillum ebenus (Lamarck, 1811)	NP	-	+	-	-
Vexillum tricolor (Gmelin, 1790)	NP	+	+	+	-
Vexillum littorale hypatiae Pallary, 1912	NP	-	-	-	+
Gibberula miliaria (L., 1758)	NP	-	+	-	-
Gibberula philippii (Monterosato, 1878)	NP	-	+	-	-
Granulina clandestina (Brocchi, 1814)	NP	-	+	-	-
Granulina sp.	NP	-	-	+	-
Conus mediterraneus Hwass in Brug., 1792	NP	-	-	-	+
Bela nebula (Montagu, 1803)	P	-	+	-	-
Raphitoma leufroyi (Michaud, 1828)	P	-	+	-	-
Raphitoma linearis (Montagu, 1803)	P	-	-	+	-
Haedropleura septangularis (Montagu, 1803)	NP	-	-	+	+
Raphitoma horrida (Monterosato, 1884)	NP	-	-	-	+

Table II. Percentage of planktotrophic (P) vs. non-planktotrophic (NP) species in the study sites. Archaeogastropods included.

Archaeogastropods included (%)				
	SPAIN	ISCHIA	DATCHA	YENIKASH
NP	58	69	69	71
P	42	31	31	29

Table III. Percentage of planktotrophic (P) vs. non-planktotrophic (NP) species in the study sites. Archaeogastropods excluded.

Archaeogastropods excluded (%)				
	SPAIN	ISCHIA	DATCHA	YENIKASH
NP	37	56	66	68
P	63	44	34	32

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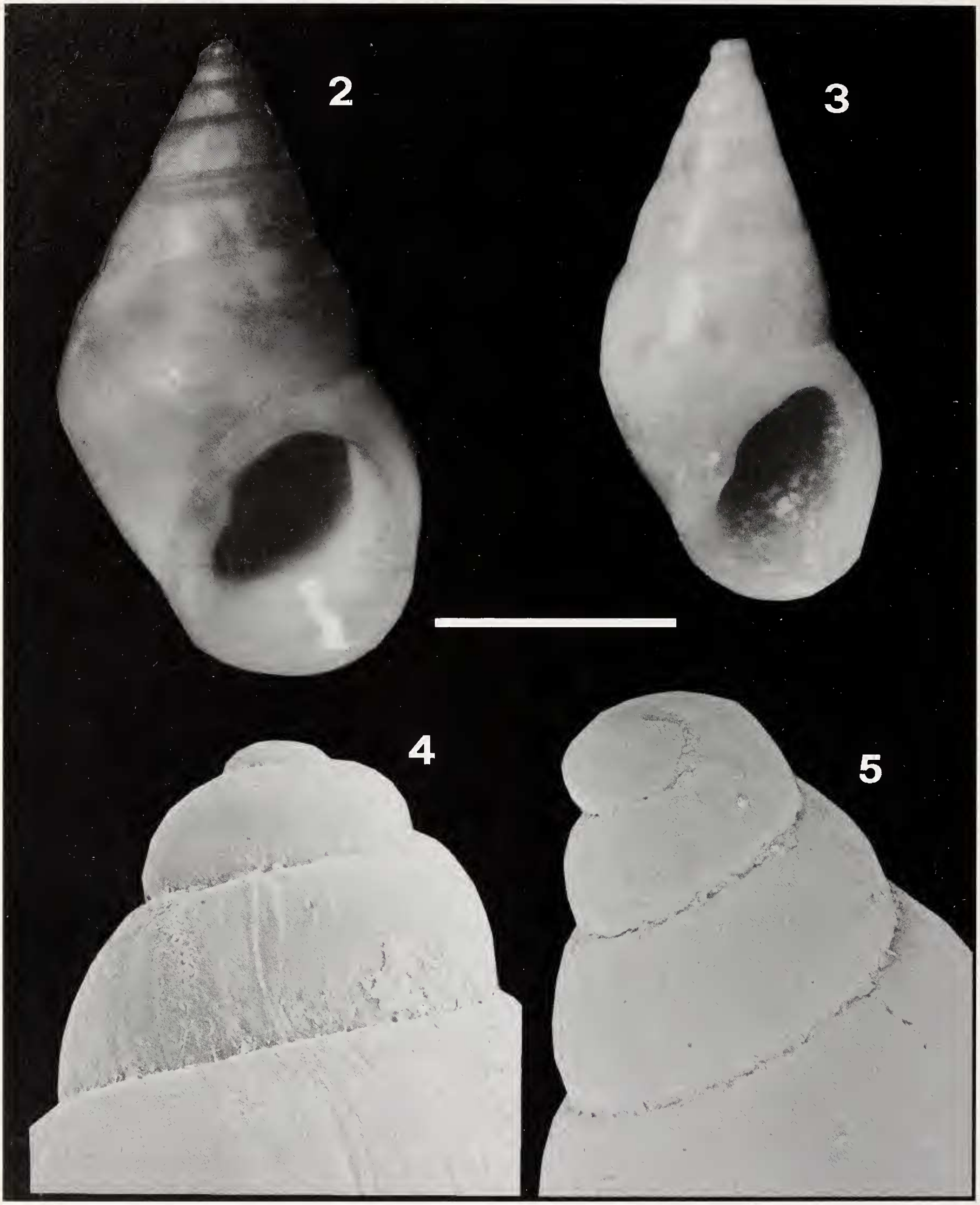

Figures 2-5. Teleoconch and protoconch of a *Rissoa* species pair. 2, 4 - *R. monodonta,* Ischia (Italy). 3, 5 - *R. auriformis,* Datcha (Turkey). Scale bar: 2 mm (2, 3), 200 μm (4, 5).